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A BASIS FOR A THEORY OF COLOR VISION.[1]

WILLIAM PATTEN, PH.D.

PART I.

THE physiologists and the psychologists have carefully studied and compared the sensations caused by ether waves of various lengths, and have attempted to explain how these manifold sensations of light and color are produced. But a satisfactory theory of color vision can never be worked out in this way, any more than a comparative study of the sensations produced by sticking different kinds of pins into the body will enable us to predict the internal sequence of events aroused by such treatment. To do that, the anatomist must first tell us what the internal mechanism is like. But he has told us very little about the retina. In fact, all that we know about its structure, either in man or in the lower animals, might be lost to science without seriously affecting the generally accepted theories of color vision. Any facts, therefore, that may possibly explain how different kinds of ether waves produce a differential response in nervous structures will be very welcome. The problem of color vision, like that of hearing, is primarily a mechanical one. We may be sure that since the stimulant that produces in us the sensation of light and color is a series of waves of definite length and frequency, the things responding to these movements must have a definite structure and position, whether they are molecules, or nervous plates, or bars, or fibrils; and their structure and position must determine the kind of waves to which they respond.

The conditions are in some respects similar to those in the ear, but they are different in so far as the cochlea possesses a series of fibres, or hairs, over which sweeps the whole gamut of sound waves, each wave length probably affecting one element only as it passes along the keyboard. In the eye, on the contrary, every point in the most sensitive part — that is, every cone — appears to possess within itself a mechanism similar to that in the whole cochlea, for it responds at the same time to almost any wave length from red to violet, or to many combinations of them.

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[1] This paper was read before the American Physiological Society at Ithaca in December, 1897. It appeared by title a year earlier on the programme of the Morphological Society, but, owing to lack of time, a five-minute abstract only was read.

It is, therefore, to the rods and cones that we must look for the solution of our problem. They are very small transparent bodies and apparently structureless. It is true that in Sir Isaac Newton's time there were supposed to be three sets of fibres in the retina, the stimulation of one set initiating mainly the sensation of red, another that of green, and the third that of blue. By combining these three sensations in various ways, it was thought that all the remaining color sensations could be produced, just as we can produce all the other spectral colors by mixing red, green, and blue light. Subsequently, various imaginary chemical compounds were substituted for the fibrils. But no evidence has been produced to show that these things exist. The physiologist "makes believe" these substances are present in the retina, but he is very careful not to say just how they should be distributed in order to produce the effects that actually are produced; or why one substance responds to one wave length more than to another; or how the single or combined responses are transmitted without confusion and loss of individuality to the cerebral centres. I believe that a reasonable answer can be given to these questions if we can only clear our minds of old traditions and look at the problem from a new standpoint.

A comparative study of the visual elements gives us this new point of departure, and we venture to offer a theory of color vision based on the fact that the rods and cones, or the parts corresponding to them in the lower animals, are not homogeneous, but fibrillated, and that in a number of invertebrates the fibrils are arranged according to their length in accurately graded series, and in such a position that they always stand at right angles to the rays of light that fall on them. The ether waves thus vibrate across a series of fibrils of different lengths.

We assume that the length and position of a fibril determine the amount of its response to an ether wave of a given length, and as each visual cone contains a complete series of these fibrils, we may understand how each cone responds to the entire series of visible ether waves or to various combinations of them; and since the rods and cones vary in shape and in size in the retinæ of different animals, or even in different parts of the same retina, there should be a corresponding variation in the length and in the number of fibrils they contain, and consequently a corresponding variation in the powers of color vision.

I shall first describe the structure and arrangement of the retinal cells in some invertebrates, omitting, of course, many details that cannot be introduced into a paper of this character. Then, assuming that the human retinal cells have a similar structure, I shall try to show how we may explain many phenomena of color vision on that basis.

More than twelve years ago I described a series of what seemed to be nerve fibrils arranged with great regularity in the rods and retinal cells of mollusca and arthropods (*Mitth. aus Neapel*, 1886). Although from time to time I have confirmed and considerably extended my original observations, no other investigator appears to have made a serious attempt to do so. But indirectly the observations have received ample confirmation, since my description of the nerve endings in the retinal cells are in complete harmony with the best recent results obtained from the study of other organs by the methylen-blue and the gold-chloride methods.

We have not found these fibrils in the rods and cones of vertebrates, but there is no good reason to doubt their existence there, since, as I shall show elsewhere, the retinal cells in both vertebrates and invertebrates agree in many important details.

Whether these fibrils in the rods are nerve fibrils in the usually accepted meaning of the term need not detain us here. It will be sufficient for our purpose if we can show that these sensory cells contain fibrils that may act as conductors or as resonators to certain kinds of movements.

The following is a very brief statement of the most important conclusions we have reached concerning the structure and arrangement of retinal cells.

(1) *Structure of a Retinal Cell.* — A typical retinal cell or retinophora, such as those found in molluscs and arthropods, although it has the outward appearance of an ordinary sensory cell, is in reality a double, or twin, cell. It consists of two nearly equal parts, readily distinguished by differences in optical properties; each part contains a nucleus and supports half of the rod (Fig. 1^1). A large nerve fibre is attached to the base of the cell and there breaks up into a dense mass of fibrils that penetrate and surround the cell and the rod. Although there is no sharp demarcation between them, we are able to distinguish three sets of these fibrils. The first set consists of comparatively coarse fibrils running lengthwise of each retinophora between its two parts; they are often closely united to form a distinct axial bundle extending into the rod and sometimes beyond its outer end. The second set ramifies over the surface of the cells and the rods. Some of them appear to be independent intercellular nerve fibres not united with the large bundle attached to the base of the cell. The third set is found mainly in the rods, where they form what I have called a *retinidium*, which consists of a series of extremely delicate transverse fibrils that appear to unite the coarser axial and the superficial rod fibres with one another. These cross fibrils give the rods either a finely dotted or a striated appearance, according to the direction from which one looks at the fibrils.

Such a retinal cell, therefore, appears to contain a mass of fibrils which extend through the center of the cell into the rods, where they bend at right angles and become continuous with those on the peripheral layers. At the base of the cell all the fibrils are gathered together to form an axis cylinder, and after extending some distance, they separate and end freely.

(2) *Position of the Visual Rods.* — The rods may be upright, inverted, or, very rarely, horizontal, as in the ocelli of some

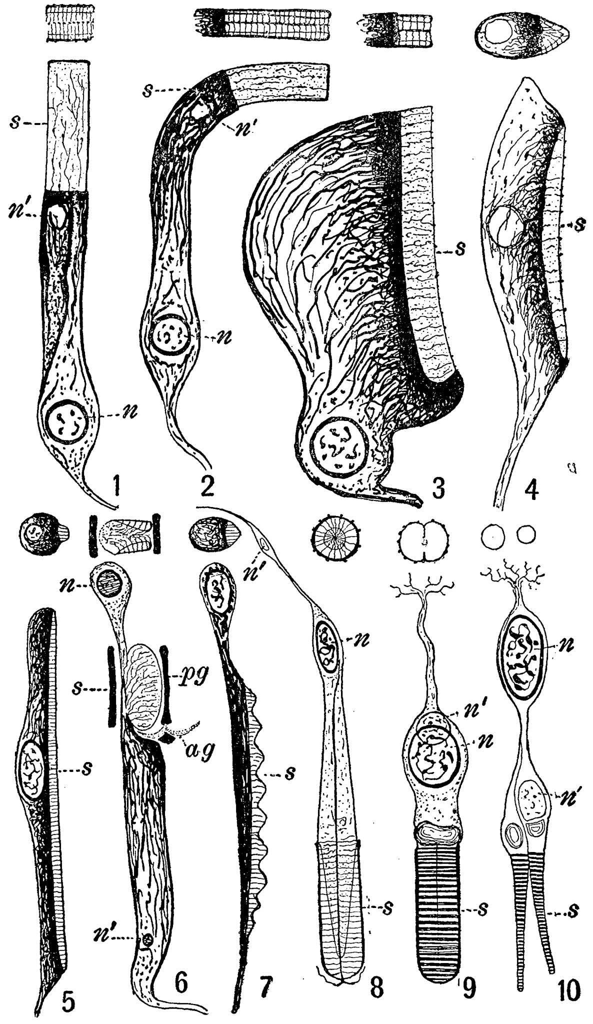

FIG. 1.—Various forms of retinophoræ, isolated by maceration and showing position and shape of retinal rods. Cross-sections of the rods are shown over each figure, the place where the section is taken being indicated by the letter *S*. 1, upright terminal rod from ocellus V of Acilius (see Fig. 2); 2, horizontal terminal rod from sides of ocellus II of Acilius (*cf.* Fig. 3); 3, a giant retinal cell with short horizontal rod from ocellus II; 4, retinal cell with lateral rod from compound eye of Limulus; 5, retinula cell from compound eye of Tabanus; 6, retinal cell from the ocellus of Lycosa; 7, retinula cell with serrated rod from the compound eye of Pinæus; 8, inverted retinal cell from the eye of Pecten; 9, rod cell from retina of an Amphibian (species of Diemyctylus), showing two nuclei, *n'* and *n*, and indications of division of rod into two parts with either a canal or fibre running through a part of the rod; 10, cone cell from same animal, showing double nature of the cell as well as of the cone. The body corresponding to the second nucleus lies at *n'*.

insects; or they may be terminal or lateral, as in either the simple or the compound eyes of arthropods. But in all cases, except the small horizontal rods of *Acilius*, the long axes of the rods are parallel to the rays of light falling on them, as shown in Fig. 1, where the light in each instance is supposed to come directly from above.

(3) *The Shape of the Rods in Cross-Section and the Arrangement of the Retinidial Fibrils.* — The shape of the rods in cross-section is a matter of great importance, because it usually indicates how the retinidial fibrils are arranged. The cross fibrils lie in superimposed planes, generally placed in one of the following positions: (*a*) When the rods are cylindrical, the cross fibrils radiate from the centre of each rod, like the bristles of a test-tube cleaner (Fig. 8, *A*, Pecten). (*b*) When the rods are quadrilateral in section, as in Acilius and Lycosa, all the cross fibrils in the same transverse plane are nearly parallel (Fig. 8, *B*, *C*, *D*). (*c*) When the rods are bound together in groups of from three to eight, as in the compound eyes of many arthropods (Tabanus, *E*, Bdellostoma, *F*, Dytiscus, *G*, Fig. 8), the angular relations of the cross fibrils will vary with the number of cells in the retinula. (*d*) In some crustacea (Penæus) the rods are serrated and dovetailed into one another in such a way that certain cross fibrils in a given transverse plane are parallel to one another, but at right angles to those in the planes above and below them (Figs. 1^7 and Fig. 8, *H*).

But whatever may be the position or shape of the rods, their retinidial fibrils always stand at right angles to the rays of light that fall on them. This is shown in Fig. 1, where all the retinal cells are seen in their natural positions. Over each figure is a cross-section of the rods, showing the direction of the retinidial fibrils. These figures, however, give only a very rough idea of the number and delicacy of the fibrils. The modifications of the shape and of the position of the rods that may occur without changing this arrangement of the fibrils are very curious and interesting, but they cannot be detailed here beyond what is given in the figures.

(4) *Position of the Retinidial Fibrils in Different Ocelli of the Same Animal.* — Where there are several pairs of ocelli in the

same animal, as in Acilius and in Lycosa (Figs. 4 and 5), the retinidial fibrils in one pair are nearly at right angles to those in two other pairs, so that the animal may be said to have its

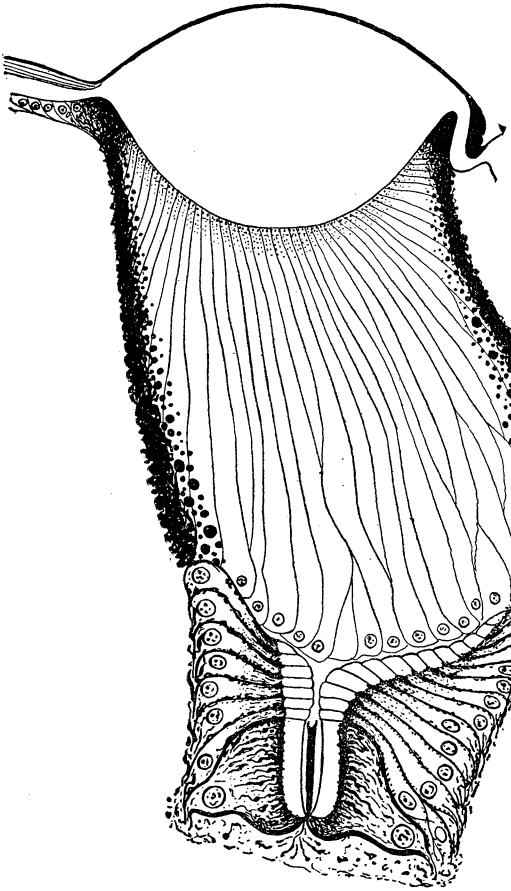

FIG. 2. — Vertical section through ocellus III of Acilius.

retinidial fibrils arranged in the three planes of space, like the hairs in the semicircular canals of the vertebrate ear. But it is a curious fact that in Acilius the pair of ocelli marked No. VI — and in Lycosa the anterior median pair — do not have their retinidial fibrils arranged in parallel lines. The arrangement of the ocelli on the right side of the head of Acilius, as seen from above, is shown in Fig. 4. One looks down into the boat-shaped retinas of ocelli I and III, the shape of which in cross-sections is well shown in Fig. 2. In these ocelli the flattened ends of the rods (shown on a larger scale in Fig. 1–$^{1-3}$) are seen as short, nearly parallel lines, the retinidial fibrils, not represented in the figures, running at right angles to them. The median band of pigment and the double row of giant rods are indicated by heavy lines. The retina of ocellus V is seen endwise, as though retina III were rotated 90° on its long axis and then stood on end, bringing the row of giant cells in a vertical position; see also Fig. 3. We therefore view the rods flatwise and lengthwise. Retinas II and IV are like those of eyes I and III, but smaller. They are placed so that the space between the two rows of giant cells lies in the plane of the paper, consequently we are looking at the giant rods lengthwise and edgewise.

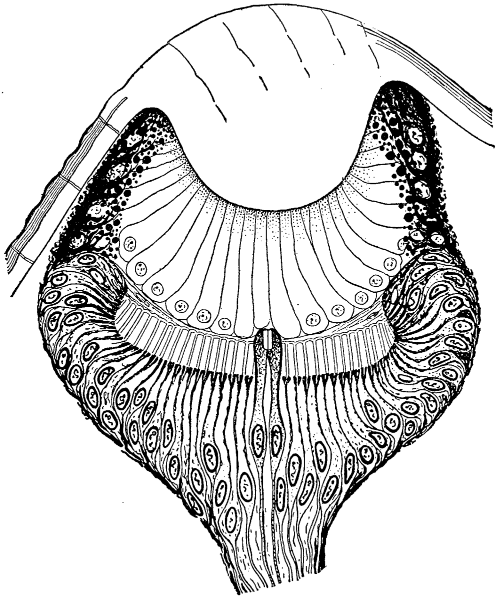

FIG. 3. — Section through ocellus V of Acilius.

In Lycosa the retinas I, II, and III show a similar orientation to the three planes of space. These three retinas are in every way similar to each other except as to size. A single retinal cell is shown in side view in Fig. 1–6 and a section of the retina in Fig. 6; this section is cut through ocellus II (Fig. 5) vertical to the plane of the paper and at right angles to the zigzag lines of pigment. On the right side of Fig. 5 these cells are shown, on a somewhat larger scale, in the three positions they occupy in the corresponding ocelli. An enlarged section nearly parallel with the surface of ocellus II (Fig. 5) is shown in Fig. 7. On the right of this figure the section plane is deeper, showing the argentea and the ends of the rod cells. A comparison of these figures shows that the rods are arranged in zigzag rows, fenced off on either side by a band of pigment, and with a concave reflecting membrane beneath each row. The rods contain parallel fibrils (Fig. 7), and they are conical both in cross and in longitudinal section (Fig. 5, I^a and II^a). The rods in the centre of the retina are very small, gradually increasing in size towards the periphery. We have here, therefore, a most beautiful arrangement, one obviously adapted to bring the rods, and the rods only, into definite relations to the rays of light.

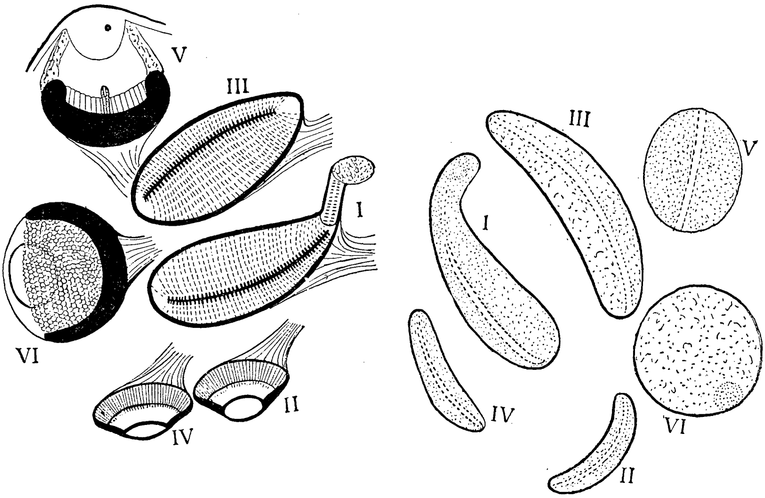

FIG. 4.— Diagram to show the arrangement of the rods in the ocelli of Acilius, and the way in which the fibrils of the optic ganglia resemble in arrangement those in the corresponding retinas.

While it is clearly an advantage to have stationary eyes directed towards the three planes of space, it is not so clear why the fibrils should be oriented to these planes. As chiten is said to be doubly refractive, it seemed probable that there was some relation between the presence in arthropod ocelli of chitenous polarizing lenses and parallel retinidial fibrils. But in the cases that I examined there was apparently no polarization in the principal axis of the lens, although I am not satisfied that renewed experiments may not give different results. In making the experiments I was strongly inclined to believe that in these ocelli the light was polarized in such a way that it would vibrate at right angles to the retinidial fibrils.

(5) *The Retinidial Fibrils are Arranged in accurately Graded Series according to their Length.* — The visual rods, in all the cases studied, could be resolved into a series of simple or compound wedges, hence the retinidial fibrils ought to vary in length according to their position in these wedges. The difference in length between the adjacent fibrils, although excessively small, should vary with the angle, and the number of fibrils in the series should vary with the altitude of the wedges.

PART II.

There is no reason to doubt that the structure of the visual apparatus in the higher vertebrates is essentially like that in the invertebrates, for we have succeeded in demonstrating that the retinophoræ in fishes and amphibia are twin cells like those of molluscs and arthropods (Fig. 1–^{9}). We can also demonstrate that the twin cone cells of amphibia are nothing more than extreme types of the same kind of cells (Fig. 1–^{10}). Furthermore, the presence of retinidial fibrils, like those of invertebrates, is clearly indicated by the well-known transverse cleavage of these rods and cones, but the fibrils themselves are probably too minute and too numerous to be clearly seen under any conditions we are as yet able to command. They are presumably arranged in distinct layers, alternating with the clear matrix of the rods and cones. Without further discussion of this point here, let us assume that the retinophoræ of verte-

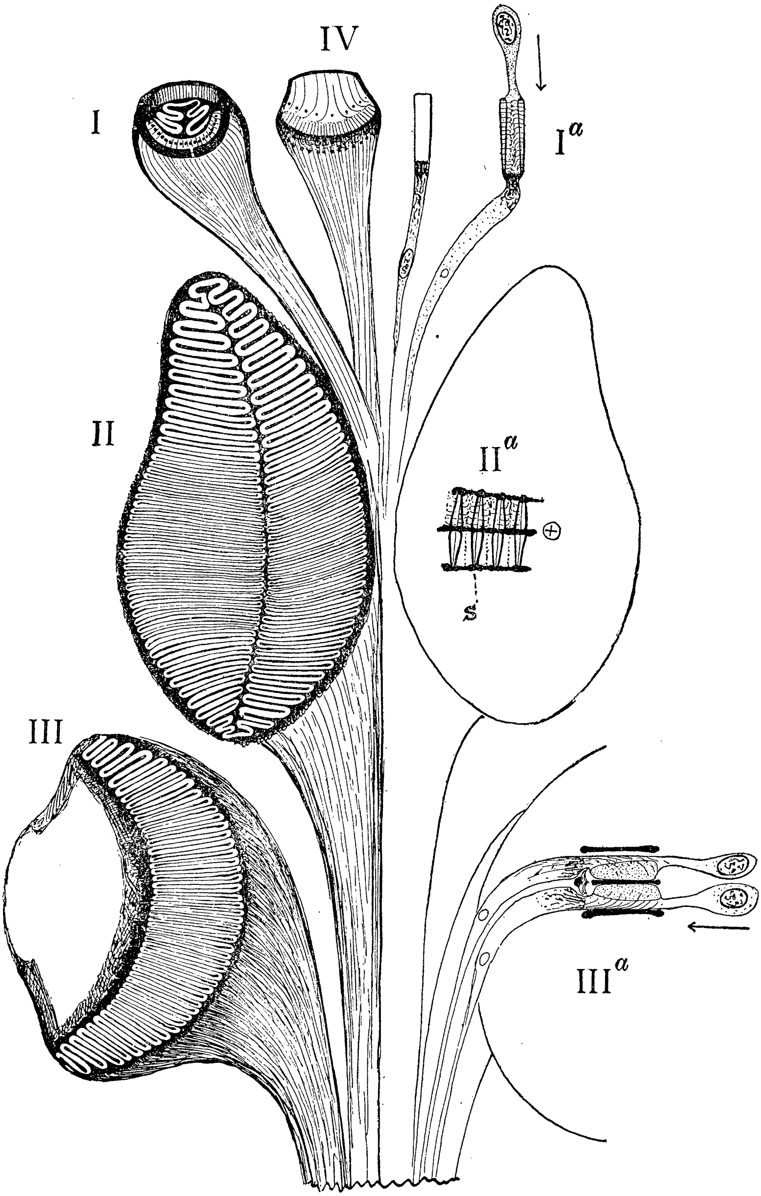

FIG. 5. — Diagram to show the arrangement of the retinal cells in the ocelli of a spider, Lycosa. The retinas, as seen from above, are shown on the left, and the position of the corresponding retinal cells, on a larger scale, on the right.

brates are like those of invertebrates, and that the retinal cones in man have a structure something like that shown in the accompanying diagrams (Fig. 9). In Fig. 9, a cone is seen in longitudinal section with the radiating fibrils on the right of the axial fibre ; on the left are projected three color curves with maxima nearly opposite *R*, *Gr*, and *V*.

Let us assume that the longest visible ether waves produce the greatest stimulation when vibrating at right angles to the longest retinidial fibrils, and the shortest visible waves produce the greatest stimulation when vibrating at right angles to the shortest fibrils. All the fibrils should be stimulated to some extent by all visible ether waves, and there should be a gradual diminution from the maximum to the minimum stimulation of any fibril according as it becomes either too short or too long to give the maximum response to an ether wave of a certain length ; or provided the fibril has the optimum length, according as it diverges from a position at right angles to the plane of vibration and to the line of propagation of the wave, toward one parallel with the plane of vibration and at right angles to the line of propagation. Now let us see what will happen if we use the simplest possible stimulant, namely, a ray of light consisting of one wave length only and vibrating in one plane, that is, a polarized ray of monochromatic light. Then let us imagine, merely for economy of words, that the fibrils most stimulated by certain ether waves become luminous with the corresponding colors. Then (1) if a ray of polarized red light passes lengthwise of the cone, it should stimulate most the longest fibrils and those most nearly at right angles to its plane of vibration and to the long axis of the cone. This should produce a band of red fibrils, brightest opposite *R*, as indicated by the thickness of the lines, and fading out above and below that level, where the fibrils become either too short or too long to make the maximum response. In a cross-section of the cone opposite *R* (Fig. 9, *B*), the fibrils at right angles to the plane of vibration, say at *a*, *b*, should be the brightest, fading out on either side towards the fibrils at *c*, *d*, which, being parallel with the plane of vibration, should be stimulated but very little, if at all.

(2) If the ray were unpolarized, there would be the same maximum stimulation at *R* as before, with a diminution of the stimulation on either side, above and below, but all the fibrils in the same transverse plane would be stimulated alike, because all the fibrils would be at right angles to at least one plane of vibration. We may, therefore, represent graphically the effects produced by a ray of polarized or unpolarized red light by the curve *r* (Fig. 9, *A*). It should attain its maximum height a little way from the base of the cone and gradually fall to zero towards the apex, where the fibrils are too short to be affected by long ether waves. The curve will fall away more rapidly at the base of the cone because the long fibrils are supposed to terminate abruptly there.

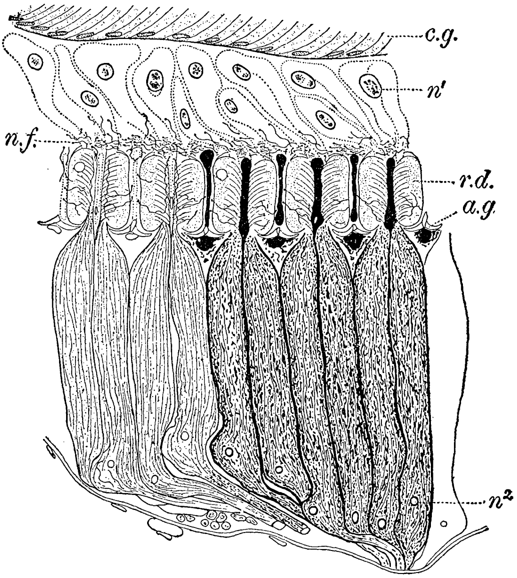

FIG. 6. — Vertical section of ocellus II of *Lycosa*. The section is cut at right angles to the rows of rods seen in Fig. 5.

(3) Similar results should be produced opposite *V* on stimulation with violet light, and of course similar results would again be produced at any intermediate point between *R* and *V* by using monochromatic light of a corresponding intermediate wave length. The stimulation curve for violet light would have

its maximum at *V* and would gradually fall away towards the base to zero. In the opposite direction the curve will be sharper, because the short fibrils terminate abruptly at the truncated apex of the cone. The curve for yellow-green light, on the other hand, with its apex opposite *Gr*, will be symmetrical because there is an equally long series of fibrils on either side of the maximum, which can respond to some extent to green light ; those on one side being too short, and those on the other too long.

(4) If a beam of polarized white light be passed through the cone, the stimulated fibrils would, if luminous, appear as two opposite spectra, wedge-shaped in cross-section, extending the whole length of the cone. All the fibrils in any one transverse plane should have the same color, but the intensity of the color should gradually diminish in those fibrils that become more and more nearly parallel with the plane of vibration. The fibrils at successive levels in the cones would of course be of different colors, and these colors would be arranged lengthwise of the cones in the same order as those in the spectrum. The gradation of colors in such a spectrum would be more or less abrupt, according to the angle of the cone and its altitude ; that is, it

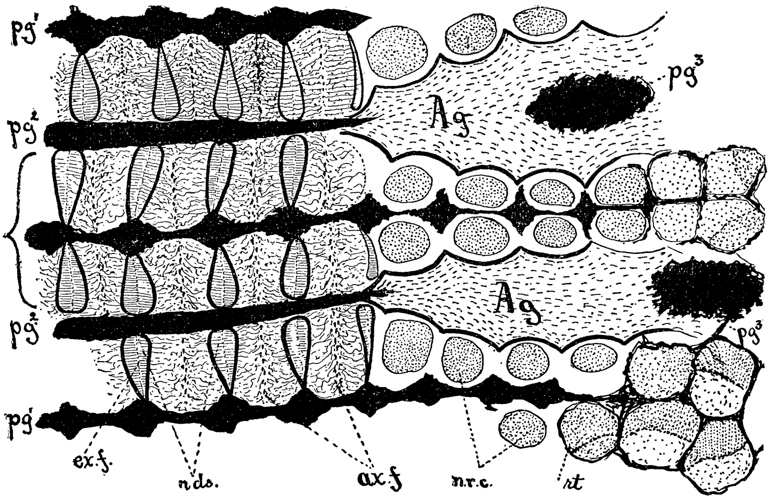

FIG. 7. — Section nearly parallel with the surface of the retina of ocellus II of Lycosa.

would be determined by the number of fibrils in the lineal series and upon the difference in length between adjacent fibrils. The precise colors exhibited at any part of the cone would depend on the length of the fibrils at that point, while the range of colors exhibited would depend on the difference in length between the longest and the shortest fibrils. But the fibrils at different levels would not be equally luminous ; first, since the physical and chemical properties of protoplasm must set a limit to the length of ether waves to which such fibrils can respond, it is probable that the fibres of medium length would respond better to their appropriate stimuli than the extremely long or short ones. And again, as already pointed out, since the series of fibrils terminate abruptly at the base and at the apex of the cones, unsymmetrical luminosity curves for the red and violet light should be produced with maxima, respectively, at *R* and *V*, while the luminosity curve of the intermediate yellow-green fibrils should be symmetrical. But since there is a double summation of stimulation in the middle region of the cones, — due to the partial stimulation of the fibrils that are shorter and those that are longer than the mean, — the

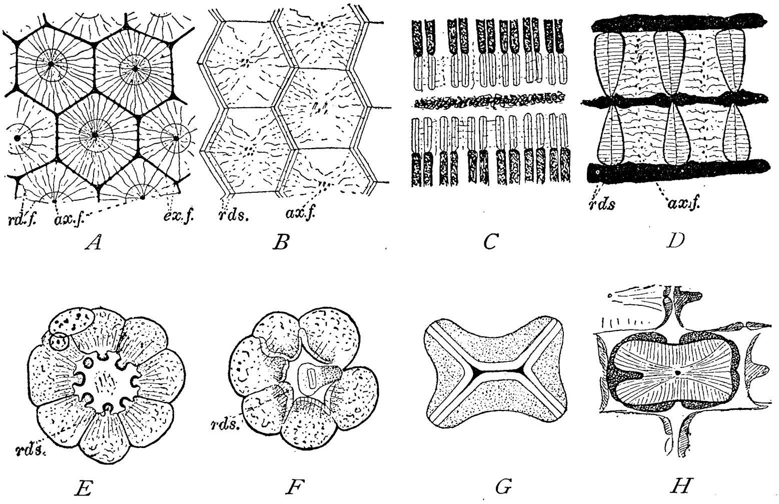

FIG. 8. — Sections through the rods of various invertebrates. *A*, Pecten ; *B* and *C*, Acilius ; *D*, Lycosa ; *E*, Tabanus ; *F*, Bdellostoma ; *G*, Dytiscus ; *H*, Penæus.

medium length fibrils should appear more luminous than those on either side of them. For this reason the middle part of the spectrum appears the most luminous, shading off on either side towards the absolute blackness of the ultra-red and ultra-violet.

(5) If we passed through the cone a ray of unpolarized white light, it should appear brighter than a polarized one, because it would stimulate all the fibrils in the same transverse plane. But in other respects the fibrils at different levels would present the same color effects as with polarized light.

(6) The sensation of whiteness is apparently the result of stimulating all the fibrils in one or more sectors of the cone to a nearly equal degree. Obviously, this may be done by passing through the cone all wave lengths from red to violet, or by selecting any two or more wave lengths at such a distance apart in the spectrum that through summation effects all the fibrils will be stimulated to a nearly equal degree. But if, for example, red and green light is selected, the place of maximum stimulation, owing to the summation of the two effects, will be at a point midway between the red and green fibrils, that is, at the level of the yellow fibres ; hence the sensation of yellow will predominate, but it will be less saturated than the pure spectral yellow.

(7) The colors visible to a given animal should depend primarily on the various diameters of the visual elements, and the range of colors visible should depend on the difference between the maximum and minimum diameters. Hence any variation in the form or dimensions of the visual elements should be accompanied by corresponding variations in color vision. For example, increasing the length of the cones should increase the total number of fibrils of all lengths in them, and hence should be accompanied by increased powers of discrimination in all parts of the visible spectrum. We may therefore attribute the increased sensitiveness of the retina at the fovea to the greater length of the cones there, for each cone is thus provided with a greater number of fibrils to respond to any wave length within the range of vision.

Again, increasing the diameter of the base of the cones should be accompanied by an increased range of vision at the red end of the spectrum. If the base of the cone were absent, red blindness should follow; but if the base of the cone should become cylindrical, with a diameter approaching that at *V* or *G*, then red blindness would follow, but accompanied by increased sensitiveness to the various shades of yellowish-green, because shortening the red fibrils would add so many more to the yellowish-green set.

We may also account for the gradual diminution in sensitiveness to red light toward the periphery of the retina by the fact that the cones, the bases of which alone contain the long red fibrils, diminish in number in that direction. On the other hand, on the outermost margin of the retina, all sense of color is lost and the sensation of black

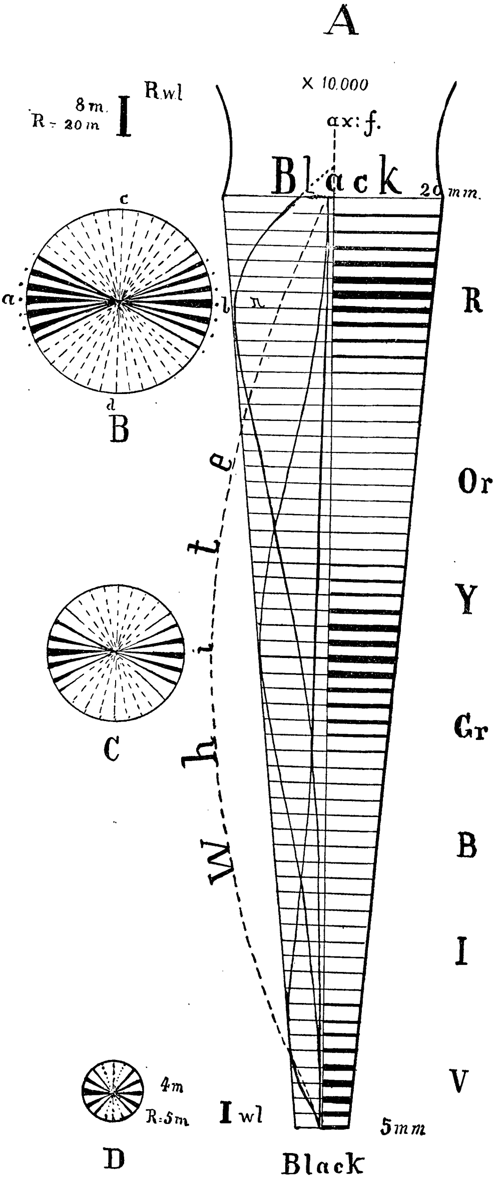

Fig. 9. — Diagram to illustrate the supposed fibrillar structure of the human cones and the way in which various light waves affect the fibrils.

and white alone remains. But this is not surprising, because towards the periphery the cones gradually disappear and the rods become the predominant elements; but since they are cylindrical bodies of uniform diameter, they must contain fibrils of one length only, — somewhat shorter than the longest cone fibrils, — consequently they cannot give rise to varied color sensations. Moreover, the periphery of the retina, judging from the manner in which the periphery grows in the invertebrates, is the youngest and least differentiated part, consequently we should not expect to find fibrils in that region which had attained just the length, position, and connections necessary in color vision.

These examples, I believe, are sufficient to show that it is a comparatively simple matter to account, from our point of view, for the more characteristic phenomena of color blindness.

(8) *The Development of Color Vision* may be explained in a similar manner. If color vision depends on the nice gradations in length or position or connection of these retinidial fibrils, the absence of these conditions should produce color blindness, but not necessarily inability to distinguish differences of light and shade. Many eyeless invertebrates react to very delicate gradations of light intensity, probably by means of the irregular networks of nerve fibrils between the epithelial cells of the naked skin. As these fibrils become phylogenetically more regularly arranged within the specialized sensory cells which serve to support them, the power to discriminate different colors should become more and more highly developed. But these conditions do not call for any particular sequence in the evolution of color sensations, for there is no reason to suppose that one set of fibrils of a given length and position would appear before another, except perhaps that a set of medium length would probably appear before the extremely short or extremely long ones, hence the sensation of yellowish-green should be the first one to emerge from that of whiteness, and subsequently it should be the most dominant and acute color sensation.

But if our views are correct, the only way in which the evolution of color vision can be worked out is by extensive measurements, much more accurate and detailed than any heretofore made, of the visual elements in all classes of animals (also in different parts of the human retina), accompanied by an experimental study of their reactions toward different colors.

(9) *Length of the Retinidial Fibrils.* — The variation in length of organic fibrils capable of responding to ether waves is rather narrow, since there is but slight variation throughout the animal kingdom in the radius of visual rods. The length of the cross retinidial fibrils, using the radius of the rods as a guide, appears to vary roughly from less than 1 to about 4μ in length (Bdellostoma). The length of the rods may vary considerably more than this, but, as already stated, this may be taken to indicate the varying number of superimposed fibrils they contain.

The length of the retinidial fibrils in any individual must be determined primarily by the physical and chemical properties of the available protoplasm without reference to any possible advantage to be derived from a response to ether waves of a particular length. For surely there is no obvious reason why animals should not utilize for visual purposes ether waves several octaves higher or lower than they do now, if only the necessary end apparatus could be produced. But since the form of the vertebral column, or of a mountain range, is the resultant of its own composition and of the forces acting on it, and since the forms actually produced are the only ones possible under those conditions, so the form and position of the retinidial fibrils must be fixed by the inherent properties of the fibrils themselves, modified by the ether waves acting on them. We may infer, therefore, that, on the whole, animals respond to all those ether waves which are capable of modeling their available protoplasm into resonant parts.

It might be fairly demanded that since the extreme red waves visible to us are about twice as long as the extreme violet ones, the longest retinidial fibrils should be approximately twice as long as the shortest fibrils. But, judging from the very unsatisfactory data at hand, they appear to be about four times as long. For example, the longest retinidial fibrils, situated at the base of the human cones, should be about .0025 mm.

long, or about three times as long as the dark red waves. The fibrils at the apex of the cones are about one-quarter as long, or .0006 mm., or about one and one-half times longer than the violet waves. These figures, of course, are comparatively rough estimates, for exact and trustworthy measurements of fresh cones are wanting ; but they will serve to show the relations existing between the probable length of the fibrils and the ether waves to which they respond.

Since there is only one kind of an impulse sent over nerve fibrils, the discrimination of different stimuli must be determined mainly by the points of departure and arrival of impulses, that is, by the particular order and combination of fibrils stimulated ; and this in turn is determined by the position and length of the peripheral end fibrils. Such an end apparatus as we have described as existing in the human retina is apparently adequate to receive and differentiate any conceivable combination of light waves that may fall within the area of one or more cones. But in order to utilize the full capacity of such an end apparatus, each and every receiving fibril should be connected by a separate wire with the central station in the optic ganglion (or *tectum opticum* of the mid-brain in lower vertebrates or *corpora quadrigemmina* of higher vertebrates), and that in turn should be united in a similar manner with the cerebral hemispheres. But the well-known limitations of the human visual apparatus clearly demonstrate that its connections cannot be as complete as this.

The same conclusions may also be drawn from the known structure of the retina itself. For while there are supposed to be about three and a half millions of cones and about one hundred and thirty million rods in the retina, there are only about half a million fibres in the optic nerve. Now, as every one knows, the fibres of the rod and cone cells extend only to the inner molecular layer, where they end freely in terminal brushes (Fig. 10) ; there the nervous impulses transmitted by these cells are probably picked up by a second set, which in turn end at the outer molecular layer ; and here the impulses are apparently again transferred to a third set, which send their fibres along the optic nerve to the optic centres. There are thus three principal sets of elements, an outer, middle, and inner, through which the nervous impulses must pass before reaching the optic ganglion. The number of elements in each set, as is obvious from even a superficial examination of the retina, decreases rapidly from the outer set towards the inner, while the territory covered by their terminal brushes increases from within outwards. In other words, one element in the middle set appears to receive impulses from many rod and cone cells, and one element in the outer set receives impulses from many elements of the middle set. There are, therefore, no indications whatever that every wave length producing the sensation of a distinct color is provided with a private wire for its sole use. On the contrary, the diminution in the number of retinal cells in each layer, and the increasing territory covered by their root-like processes as we pass from the outer surface of the retina inward, indicate very clearly that the so-called ganglionic layers do not serve to still further

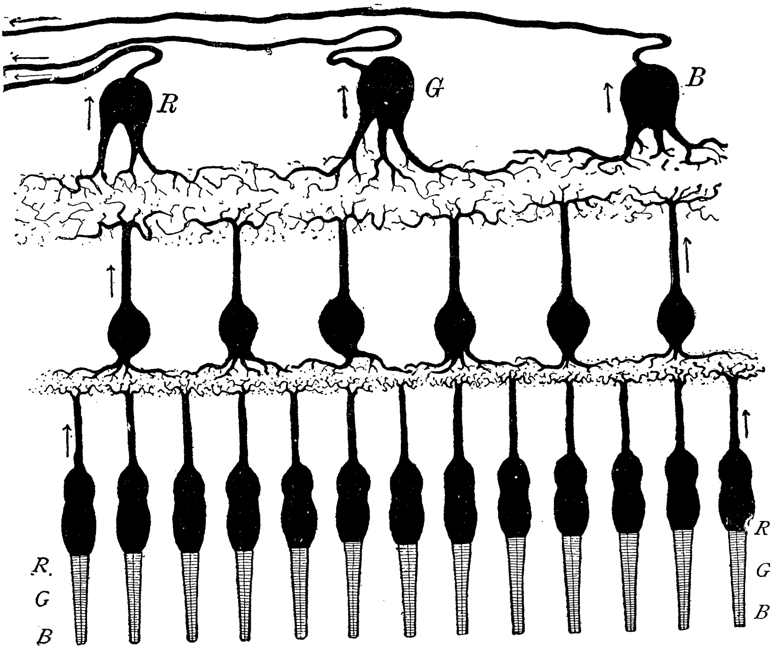

Fig. 10. — Diagram to illustrate a possible mode of convergence of retinal impulses in the human retina.

complicate the processes going on within the retina, but rather to simplify them, in that they make it possible for the fibrils of the same length in many adjacent rods or cones to deliver their impulses into gradually converging channels.

Many questions arise in this connection that it is as yet hardly profitable to discuss, as, for example : How large an area of rods and cones is tributary to a single optic nerve fibre ? Are these areas distinct or do they overlap each other ? And, further, to what extent is there a qualitative analysis of impulses previous to convergence ; that is, are all the sensations initiated in the long red fibrils of, say, three hundred cones transmitted by a single axis cylinder of the optic nerve, and if something of this kind takes place, is it true only for the red, green, and blue sensations or for ten, or twenty, or more different sensations ? But whatever the answer to these questions may be, that there must be, on any theory, some kind of convergence of impulses from the rods and cones towards the optic nerve, is decisively demonstrated by the numerical relations between the rods and cones in the ganglionic cells and the fibres of the optic nerve.

Certain facts appear to indicate that there is a qualitative as well as a quantitative convergence. It is well known, for example, that the stimulation of an area as small as the base of a single cone may produce the sensation of light, but that a considerably larger area must be stimulated before the sensation of any distinct color is produced. This fact is apparently correlated with the distribution of the large ganglion cells of the inner layer, because these cells are more numerous around the fovea than on the periphery of the retina, indicating that there should be less convergence of impulses there than at the outer margin, where one ganglion cell of the inner layer must collect the impulses from a very large number of rods and cones. This appears to be the case, for we can distinguish the colors of small objects better with the centre of the retina than with the periphery; or, rather, small objects which barely produce the sensation of a distinct color when seen with the centre of the retina must be considerably increased in size in order to produce this effect when seen with the periphery.

But what is the disposition of the impulses after leaving the retina? They, of course, follow the optic nerve fibres to the optic ganglion and pass from there to the cerebral hemispheres. But why should we have these two internal centres? The conditions in Acilius furnish a partial answer, I believe, to the question. In the larvæ of this insect there are six pairs of ocelli, and each ocellus happens to have a characteristic size, shape, and arrangement of retinal cells. The nerves to the ocelli unite to form a common nerve, which near the optic ganglion again separates into six nerves, each one ending in a distinct mass of fibrillated substance. These masses of "*Punct-Substanz*" present such a striking resemblance in relative position, size, form, and structural details to the corresponding retinas that there cannot be the slightest doubt as to which ocellus each medullary core belongs. It is not claimed that there is absolute agreement between the retina and its mass of *Punct-Substanz*, but the resemblance goes so far that the singular appendage to retina I, the median furrows in retinas I to V, and the absence of this furrow in the circular retina of ocellus VI, together with the presence of a peculiar patch of inverted cells, are all represented in the corresponding part of the optic ganglion by some change in the number or arrangement of the fibrils. This is a fact of fundamental importance, and while it has been observed only in this instance where the conditions are especially favorable, the principle probably holds good for other animals as well. This similarity between the inner and outer extremities of the visual apparatus indicates that the *Punct-Substanz* of the optic ganglia consists of a series of fibrils which in their numbers and general arrangement agree with the retinidial fibrils to which they are united; and it also indicates that a series of changes initiated by light in the retina are re-presented in the optic ganglion by another sequence of changes having time and spacial relations similar to those in the retina. The whole apparatus is comparable with a telephone, or with a Marconi transmitter and receiver. As the structure of such end organs must be to a certain extent created by the ether waves that rouse them to activity, so the structure and adjustments in the optic ganglion must be determined in part by the impulses they receive from the retina, just as certain joints, for example, have been produced by repeated stresses and movements of a particular kind. But when such joints are once established, they permit only those kinds of movements that were most instrumental in producing them, whatever may be the nature of the stimulus that initiates these movements. It is, therefore, probable, when certain adjustments have once been established in the optic ganglion through repeated retinal stimulation, that any stimulation of such a collection of fibrils might call forth the particular series of activities necessitated by such an adjustment, whether the initiatory impulse comes from within or from without. In other words, the existence of a second visual centre, or optic ganglion, having a structure similar to that of the retina, may be considered as essential in establishing for past experiences latent records, which can be brought again into activity through other stimuli than those that originally produced them. We are thus provided with a physical basis for the explanation of hallucinations and for certain phenomena of visual memory.

It is clear from known anatomical relations that the visual impulses do not cease at the optic ganglion, but are transmitted to other centres in the cerebral hemispheres, provided such hemispheres are present. While there is no animal in which the optic ganglion is not united with the anterior part of the brain, it is apparently only in the higher arthropods and in the vertebrates that it is united with a definite part of the cerebral lobes. In Limulus and scorpions, where I have made a special study of these conditions, the cerebral visual centres do not resemble in any way the optic ganglia or the retina, but their whole appearance indicates that they consist of masses of cells and fibres that serve to bring the nervous impulses received from the eyes and optic ganglia into relation with various parts of the body.

We are thus led to conclude from a comparison of widely different types of animals that the visual apparatus consists of three principal parts, which phylogenetically are developed in the order named, *viz.:* the *retina*, or receiving centre; the optic ganglion, or recording centre; and the cerebral portion, or the coördinating and distributing centre. The structural unit of this apparatus appears to be a fibril, many hundreds of which may be present in each rod or ganglion cell. As the retinidial fibrils appear to form loops in the cones by uniting axial and external fibrils, and their central extremities terminate freely, it is possible that the retinal fibrils form elongated ∩-shaped loops, which might be compared to excessively small Hertz's resonators, the spaces between the ends of the fibrils representing the spark gaps. But whatever comparison may be made between these fibrils and any electrical device, it is not to be assumed that they actually vibrate, like tense strings, in harmony with ether waves. But while they presumably act mainly as conductors and resonators, that fact would not exclude their undergoing metabolic changes, resulting in central or peripheral fatigue or temporary exhaustion.

DARTMOUTH COLLEGE,
HANOVER, N. H.